

THE IMPACT OF FLOWER HARVESTING ON SEEDLING
RECRUITMENT IN SEA LAVENDER
(*LIMONIUM CAROLINIANUM*, PLUMBAGINACEAE)

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ABSTRACT. Flowers of *Limonium carolinianum* are harvested for use in dried flower arrangements and various crafts. The increasing commercialization of this harvest has led to concerns regarding its sustainability. We quantified the extent of the harvest on four marshes on the Bay of Fundy coast of Nova Scotia, Canada. Over a four-year period from 1996 to 1999, flower stalk removal averaged 32% on easily accessible portions of these marshes (i.e., within 100 m of a road) compared to 5% on inaccessible portions (greater than 500 m from a road). In 5 × 5 m plots where flowers were experimentally removed, no seedlings emerged the following year, whereas seedlings always emerged in unpicked control plots. This rapid and dramatic impact of localized harvesting on seedling emergence is due to the limited dispersal and short life span of *L. carolinianum* seeds. Sampling in concentric circles around isolated adults revealed that 50% of seedlings emerged within 34 cm of the parent and 90% emerged within 61 cm. Tethered seed experiments revealed that seeds that did not germinate in the first spring after production did not survive to the next spring. Our results suggest that unregulated harvesting has the potential to dramatically impact recruitment into local populations. To reduce the likelihood of local extinction we recommend that harvesters do not reduce flower stalk densities below 1 per m².

Key Words: *Limonium carolinianum*, flower harvesting, salt marsh, seed bank, seed dispersal, local extinction, sustainable harvesting

Limonium carolinianum (Walter) Britton, Plumbaginaceae (sea lavender) is a long-lived perennial herb that ranges the entire eastern coast of North America from Newfoundland to Texas (Roland and Smith 1983). Inflorescences of this species are collected and dried for use in floral arrangements and various crafts. Small-scale harvesting by individuals has a long history within

Atlantic Canada. Given that *L. carolinianum* is fairly common on salt marshes and beaches, such small-scale harvesting may have little impact on populations. However, due to the current popularity of the flowers and recent larger-scale commercial harvest of them, there is a growing concern about the effects of harvest (see article by Jim Wolford in the May 26, 1996 edition of the Advertiser and article by Jodi DeLong in the September 3, 1996 edition of Shunpiking). Local landowners have suggested to us that there have already been population declines on some heavily exploited salt marshes in Nova Scotia.

The historic loss of salt marsh habitat has also impacted on *Limonium carolinianum* populations. In Nova Scotia it is estimated that 57% of all salt marsh has been lost due to dyking for agricultural use and erosion caused by dredging and filling (Hatcher et al. 1981). Much of what remains is highly fragmented with many pockets of salt marsh being less than 10 hectares in size (Eaton et al. 1994). Depending upon how widely this species disperses, this fragmentation has the potential to further exacerbate the effects of local harvesting.

Because of these concerns, we conducted a study to determine: 1) the current level of harvest in salt marshes along the Bay of Fundy coast in Nova Scotia, and 2) the impact of this harvest upon recruitment into the local population. We addressed the first objective by enumerating flower stalks in permanent plots before flower opening, and again after seed set, in four relatively accessible and four relatively inaccessible salt marshes over a period of four years. Since the impact of flower harvesting upon recruitment in any one location and in any one year will vary depending upon how widely seeds are dispersed and the extent to which seeds may be stored in the seed bank, we collected basic data on both these parameters. Finally, we experimentally assessed the impact of harvesting on seedling emergence by removing flower stalks from controlled plots and examining the impact the following year.

Although the focus of this study was on the effect of harvesting on seedling recruitment, it should be recognized that the importance of seedling recruitment in determining population growth rate has yet to be determined in this species. However, regardless of how closely seedling recruitment is linked to population growth rate, an understanding of the effect of harvesting on this parameter is important as it is the primary mechanism by which

this species disperses, and by which genetic diversity within the population is generated.

MATERIALS AND METHODS

Study species. *Limonium carolinianum* inhabits salt marsh and both rocky and sandy beaches. Individuals have leathery, succulent leaves, arranged in a basal rosette around a compressed stem that is attached to a central taproot. Inflorescences are produced on scapose stems. They first appear in early July and develop into highly branched stalks with many small purple flowers by mid-August. Flowering can continue as late into the fall as October. Breeding experiments have shown *L. carolinianum* to be self-compatible, and individuals bearing both selfed and outcrossed seeds are found in the wild (Hamilton and Rand 1996). Each flower can produce up to four seeds, but normally produces only one. *Limonium carolinianum* is also capable of limited clonal growth through the addition of ramets to the underground stem. However, ramets remain permanently attached to the central taproot and never give rise to physiologically independent clones. As a result, individual plants vary widely in size and can have from 1 to 20 or more inflorescences.

Study sites. The individual studies described below were conducted at one or more of the following salt marshes: Kingsport (45°09'N, 64°22'W), Avonport (45°7'N, 64°16'W), Annapolis Royal (44°44'N, 65°32'W), Porter's Point (45°08'N, 64°23'W), and Wolfville (45°05'N, 64°21'W). These five marshes were chosen for three reasons: 1) based upon their floristic composition and zonation patterns they are typical of salt marshes in Nova Scotia (Davis and Browne 1996), 2) they were large enough to allow replication of the study plots, and 3) they provided a range of geographic locations along the Bay of Fundy coast of Nova Scotia. Due to time constraints, those studies that required frequent visits to the field were all conducted at a single site, the Wolfville salt marsh. We make the assumption that the data collected at this one site is representative of the remaining sites.

Extent of harvest. To assess the extent that harvesters were exploiting populations of *Limonium carolinianum* at the time of the study, we established plots in Kingsport, Avonport, Annapolis

Royal, and Porter's Point. Plots were established on parts of the marsh that were either easily accessible or relatively inaccessible to harvesters. A plot was considered accessible if it was within 100 m of the nearest road, and inaccessible if it was greater than 500 m from the nearest road. Plots were 5 × 10 m in size and were marked by wooden stakes at each of the four corners. The stakes extended only 30 cm above the surface of the ground and were largely hidden by the surrounding vegetation. Therefore, it is unlikely that they were conspicuous enough to discourage people from harvesting in that area. Three plots were established on both accessible and inaccessible sites on the Kingsport, Avonport, and Annapolis Royal marshes in 1996. Two additional plots were established at each of the original sites, and another five plots established on accessible and inaccessible sites on the Porter's Point marsh in 1997. From 1996 to 1999, the number of flower stalks in each plot was counted prior to flower opening (late July/early August) and again after flowers had withered (September/October). During the latter census we also noted whether there were any indications that flower stalks had been harvested, by looking for the remains of cut flower stalks still attached to the plants. Due to time constraints not all of the inaccessible sites were sampled in all years.

Seed dispersal. Ten adult plants were selected on the Wolfville salt marsh in June 1999 after natural emergence in the field had terminated (see below). Circular, 2 cm wide belt transects were set up at 10 cm intervals from the adult plant and the number of seedlings in each transect was counted. Sampling continued outward from the mother plant until three consecutive transects without seedlings were sampled. The seedling density for each band was calculated and the total number of seedlings at a given distance from the parent was determined through interpolation between bands.

The above procedure assumes that all seedlings encountered in the circular transects were the progeny of the single adult at the center of the plot. To help ensure the validity of this assumption, only adult plants that were a minimum of 3 m from their nearest neighbor were chosen for this study. This distance was chosen on the basis of preliminary observations of the diameter of the seedling "shadow" surrounding individual plants.

Seed longevity in seed bank. To help interpret the results of the seed longevity experiment (see below), the pattern of natural seedling emergence over the course of the growing season at the Wolfville salt marsh was examined. In May 1997, twenty 15 × 15 cm plots were established at randomly selected points in a subsection of the marsh with a high density of adult *Limonium carolinianum*. At first emergence, all seedlings in each plot were counted and removed on an approximately weekly basis until emergence ceased. The plots were censused again in 1998 and 1999. In 1997 and 1998, the plots were also censused in October/November to determine if any emergence occurred in the fall.

To assess how long *Limonium carolinianum* seeds can remain viable under field conditions, naturally ripened seeds were collected from the Wolfville salt marsh in the spring and fall of 1998, and placed in 10 × 10 cm fine-mesh nylon bags (25 seeds per bag). Bags were placed back on the salt marsh for varying lengths of time under one of three conditions:

1. tied to a wooden stake at a height of 30 cm to simulate seeds that fail to shatter and remain in the seed stalk;
2. fastened to the surface of the soil, using nails placed at each of the four corners of the bag, to simulate seeds that shatter and remain on the soil surface;
3. buried at a depth of 2.5 cm to simulate shattered seeds that have been buried by mud washed in by the tide.

Seeds collected in the fall of 1998 were stored dry in the laboratory at 3.5°C until being placed back on the marsh on December 10, 1998 or June 22, 1999 (i.e., after natural emergence had terminated). Seeds collected in the spring of 1998 (i.e., from seed stalks that had overwintered) were placed back on the marsh on June 4, 1998, again, after natural emergence had terminated. In the case of seeds placed on the marsh in June, the treatment simulating seeds that failed to shatter was omitted, as by this time all seeds had naturally shattered. Seeds placed on the marsh on June 4, 1998 and December 10, 1998 were collected on April 10, 1999, and seeds placed on the marsh on June 22, 1999 were collected on July 7, 1999. There were 20 seed bags (replications) per treatment per date of collection.

At the time of collection, the number of seeds in each bag that had already germinated was noted and the remaining seeds placed

in petri dishes on moist Kimwipes soaked in distilled water. The petri dishes were wrapped in parafilm to minimize water loss and placed in a growth chamber that provided a 14 hr. photoperiod and a 20/15°C day/night temperature. Germination was monitored daily until a period of five days had passed in which there were no new germinates, at which time the remaining seeds were tested for viability using tetrazolium chloride (Delouche et al. 1962).

None of the seeds that failed to germinate in the growth chamber were found to be viable using the tetrazolium test. Therefore total viability was calculated as the sum of germination in the field and in the laboratory expressed as a percentage of the total number of seeds originally placed in the field. As the resulting percentages were not normally distributed, a Kruskal-Wallis test was used to examine differences in field germination and total viability among treatments.

Effects of bloom picking on seedling recruitment. On July 15, 1998, twenty 5 × 5 m plots were established in an inaccessible region (i.e., > 500 m from the nearest road) of the Wolfville salt marsh that also had a high density of *Limonium carolinianum*. Ten plots served as unmodified controls, while in the other 10 plots all flower stalks were removed. Treatments were assigned randomly to plots. The following spring after seedling emergence was complete (see above), seedling density was sampled as described in the seed dispersal survey. A point was randomly selected within each plot and the nearest adult was used as the center for the circular belt transects. In most cases the nearest plant was part of a cluster of several plants. In these cases, the focus for the circular transects was the center of the entire group of plants and the total number of plants in the cluster was determined. Sampling was done at 10 cm intervals from the center to a distance of 100 cm. These data were used to estimate the total number of seedlings within the sampled area (i.e., a circle with a radius of 100 cm). The effect of bloom removal on seedling density was examined using analysis of covariance with the number of adults in the plots as the covariate.

RESULTS

Extent of harvest. Averaged across sites and across years, 32% of flower stalks were harvested from accessible plots com-

Table 1. Extent of *Limonium carolinianum* harvest on accessible versus inaccessible parts of four marshes along the Bay of Fundy coast in Nova Scotia from 1996 to 1999. Harvest was quantified by counting the number of flower stalks in permanent plots prior to flower opening in the summer and again in the fall after flowers had withered. There were 3 plots per site in 1996 and 5 plots per site in all other years. Not all sites were censused in all years. Asterisks indicate that the remains of cut flower stalks were observed.

Marsh	Percent of Flower Stalks Removed (\pm SE)			
	1996	1997	1998	1999
Avonport				
Accessible	91 \pm 3*	15 \pm 7*	35 \pm 12*	33 \pm 10*
Inaccessible	—	14 \pm 15	16 \pm 11	17 \pm 21
Annapolis Royal				
Accessible	29 \pm 11*	48 \pm 14*	28 \pm 9*	42 \pm 15*
Inaccessible	—	—	-8 \pm 7	—
Kingsport				
Accessible	5 \pm 3	29 \pm 13*	15 \pm 11*	8 \pm 3
Inaccessible	4 \pm 4	1 \pm 3	3 \pm 5	—
Porter's Point				
Accessible	—	39 \pm 12*	23 \pm 9*	33 \pm 9*
Inaccessible	—	—	-6 \pm 7	—

pared to 5% from inaccessible plots (Table 1). Direct evidence of bloom harvesting in the form of cut flower stalks was observed in the accessible portions of all four marshes (13/15 plot-year combinations), but was never observed in the inaccessible portions (0/8 plot-year combinations). The level of harvest on accessible plots varied substantially from marsh to marsh and from year to year. The greatest range among years was observed at Avonport where the level of harvest ranged from 15 to 91%. The range in harvest levels for accessible plots at Annapolis Royal (28–48%), Kingsport (5–29%), and Porter's Point (23–39%) was less than that observed at Avonport, but still substantial. The range in harvest levels on the inaccessible plots was much less than that observed for the accessible plots. At the two sites where we sampled the inaccessible plots over multiple years, Avonport and Kingsport, the ranges in harvest levels were 14–17% and 1–4%, respectively.

Seed dispersal. The highest seedling densities were observed at approximately 20–30 cm from the mother plant (Figure 1). No

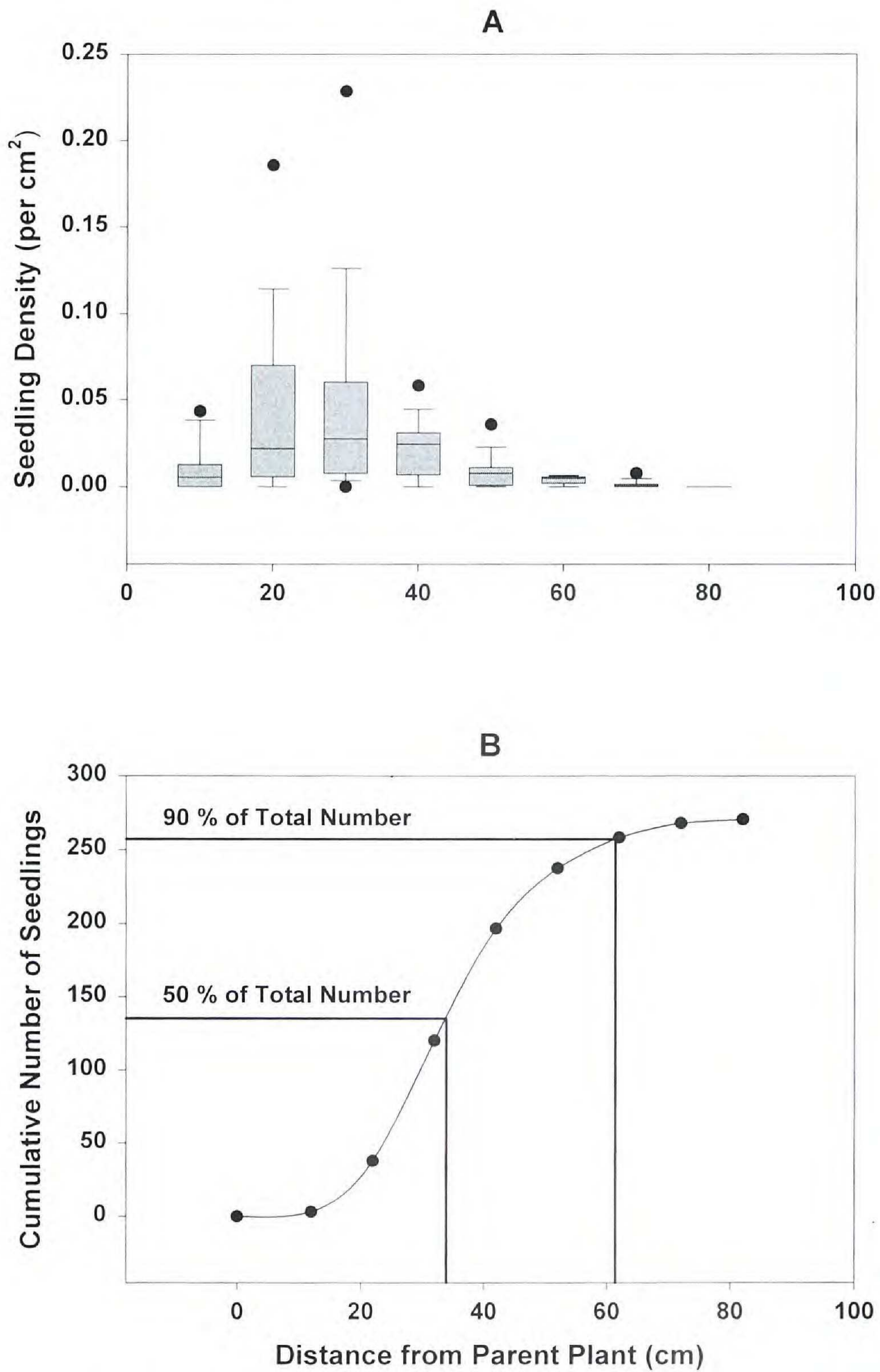


Figure 1. Seedling density (A) and cumulative number of seedlings (B) as a function of distance from 10 isolated parent plants. Densities in (A) are graphed in a box plot that displays the 10th, 25th, 50th, 75th, and 90th percentiles as well as any outliers.

seedlings were observed further than 80 cm from the mother plant. On average, 50% of the seedlings were within 34 cm and 90% of the seedlings were within 61 cm of the parent.

Seed longevity in seed bank. Natural seedling emergence began in early spring, from mid-April to early May depending upon the year (Figure 2). Emergence was highly synchronous within years, with most of the seedlings emerging within a two-week period. Emergence was essentially complete by mid-May in 1998 and 1999, but extended into early June in 1997. We observed no seedling emergence in the fall.

Freshly ripened seed collected in the fall germinated readily under laboratory conditions; on average, 97% of the seeds germinated (Figure 3). Seed viability decreased after overwintering on the marsh, but the extent of this decrease varied depending upon location (Kruskal Wallis test, $X^2 = 15.01$, $p = 0.005$). Buried seed had the highest viability and seeds that were staked above the ground (simulating seeds that remained on the seed stalks) had the lowest viability. Field germination in the spring was even more dependent upon location of the seeds (Kruskal Wallis test, $X^2 = 25.84$, $p < 0.0001$). Most of the buried seeds germinated in the field, while very few of the seeds staked above ground germinated; germination of the seeds placed at the soil surface was intermediate between that in the other two treatments. Seeds that were placed on the marsh after natural emergence ended in the spring did not germinate in the field, but when brought into the laboratory later that summer had a viability only slightly below that of seeds before the flush of spring emergence. However, there was no evidence that the remaining treatments (buried versus soil surface) had any effect on viability (Kruskal Wallis test, $X^2 = 0.19$, $p = 0.6646$). Seeds that were placed on the marsh after the flush of spring emergence were no longer viable the following spring.

Effect of bloom picking on seedling recruitment. No seedlings were found on the 10 picked plots, but seedlings were observed on all 10 unpicked plots (Figure 4). Seedling densities in the unpicked plots were highly variable. An analysis of covariance revealed that much of this variability was correlated with the number of adults in the plots ($F = 5.57$, $p = 0.0313$).

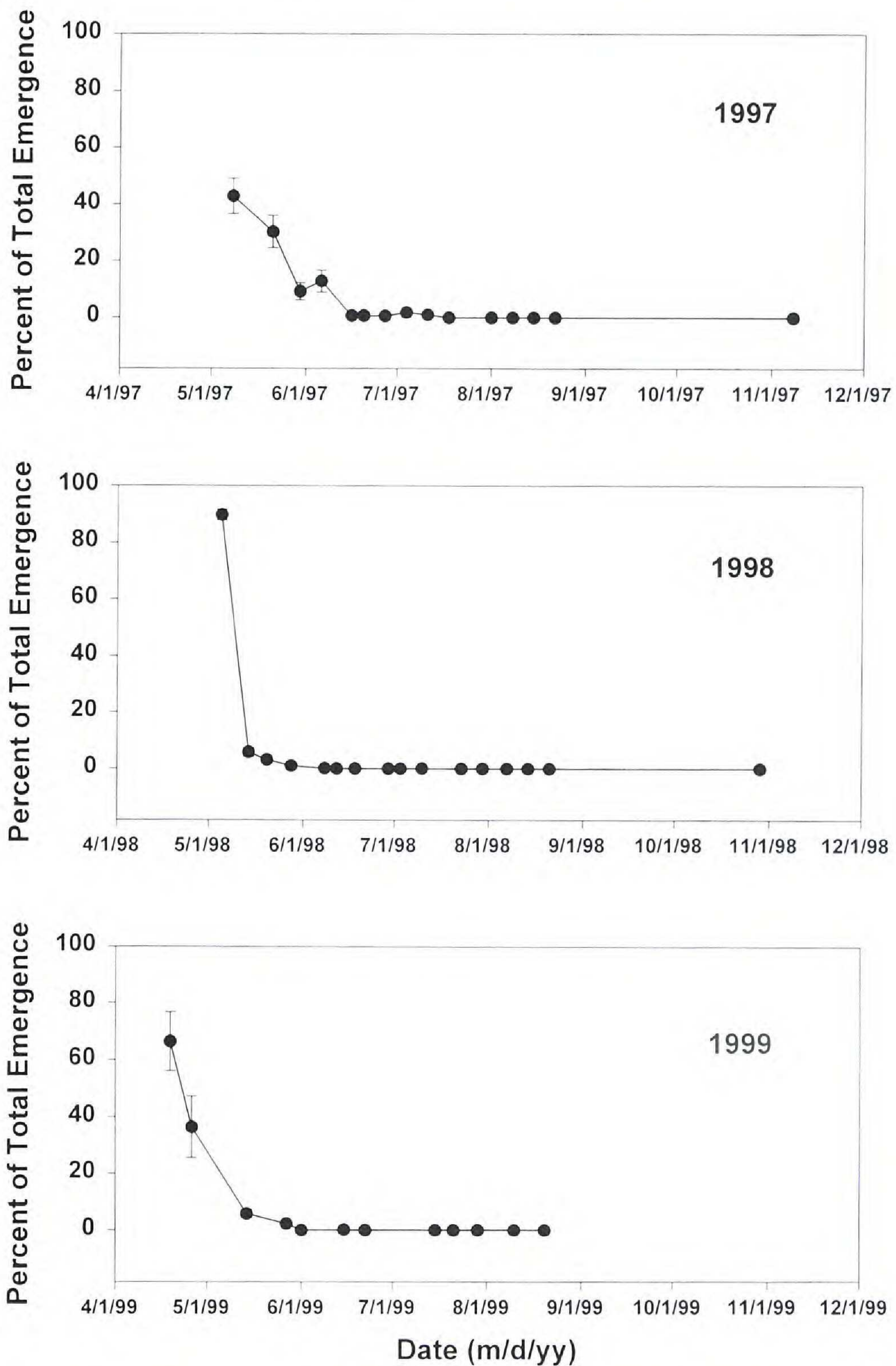


Figure 2. Percent of total seedling emergence over the course of the growing season on the Wolfville salt marsh in 1997, 1998, and 1999. Points are the mean of 20 plots (± 1 SE).

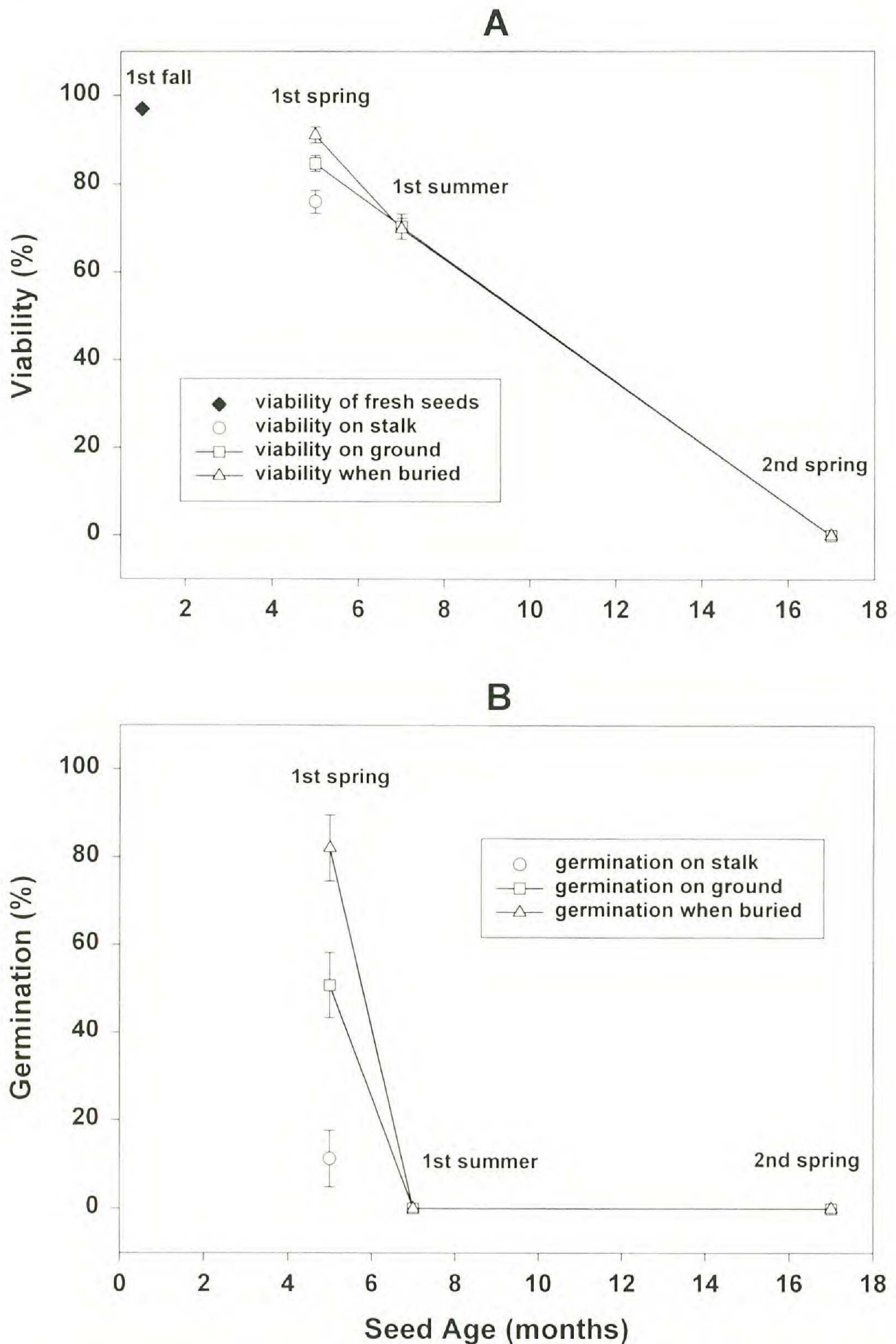


Figure 3. Percent viability (A) and percent germination in the field (B) of seed collected from the Wolfville salt marsh, placed in fine-mesh nylon bags, and returned to the marsh for various lengths of time. To simulate the environment of seeds still attached to the seed stalk, seeds on the ground surface, and seeds buried beneath the ground, the bags were placed at one of

It also revealed that the effect of picking on seedling density was highly significant ($F = 9.45$, $p = 0.0073$).

DISCUSSION

The current harvest of *Limonium carolinianum* flower stalks is variable in both time and space, varying from year to year, marsh to marsh, and even within a marsh depending upon accessibility to harvesters (distance to the nearest road). Importantly, the level of harvest at a particular time and location can be extensive, in one particular case exceeding 90%. The long-term impact of such a harvesting regime on a local population will depend, at least in part, upon how well the species is able to disperse through time and space. If the scale at which seeds disperse is greater than the scale of the harvested patches, or if seeds remain viable within the seed bank for a length of time greater than the average time between harvests, periodic heavy harvesting may have relatively little impact on the local population. This does not appear to be the case for *L. carolinianum*.

The scale over which *Limonium carolinianum* seeds disperse is relatively small. No seedlings were found further than 80 cm from the parent plant. Given that many of the seeds remain attached to the inflorescence over winter (pers. obs.), this limited dispersal is not surprising. Most seeds appear to simply fall in a small area directly underneath the seed-bearing portion of the inflorescence. The inflorescences tend to bend to one side prior to shattering, probably due to tidal action, resulting in a seed rain displaced to one side of the mother plant, with maximum seedling density occurring approximately 30 cm from the plant. This distance corresponds well with the height of the seed stalk.

Although the seedling distribution data suggest dispersal on a very limited scale, this species is likely capable of dispersing to much greater distances under some circumstances. A sample of 100 seeds threshed by hand from inflorescences collected in the

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three locations: 1) tied to a stake at a height of 30 cm, 2) tacked to the ground surface, or 3) buried 2.5 cm beneath the surface. In calculating seed age, it was assumed that all seeds matured on November 10. Points are the mean of 20 values (± 1 SE).

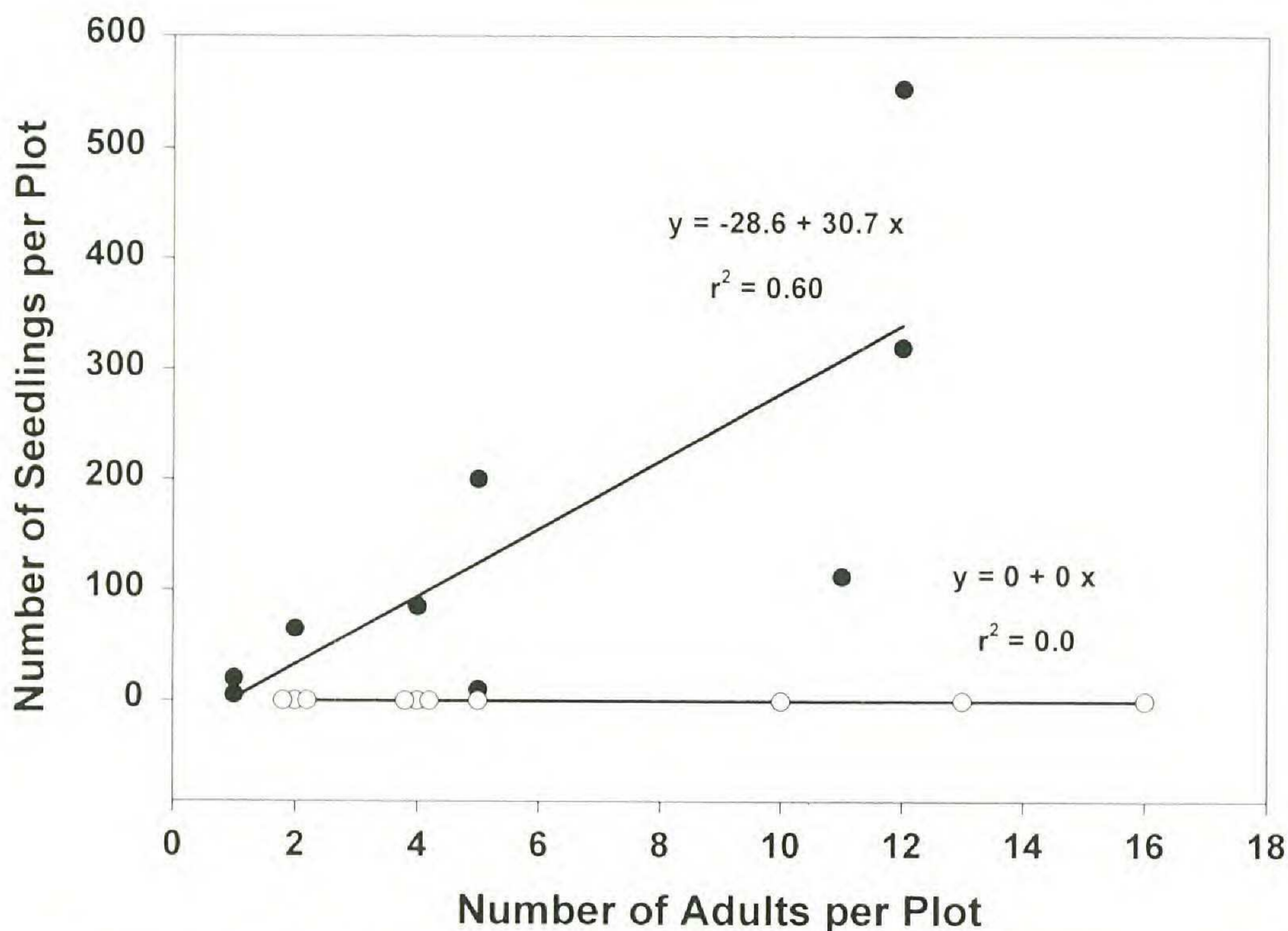


Figure 4. Number of seedlings per plot as a function of the number of adults per plot for control (closed symbols) and harvested (open symbols) sites. X-axis points are jittered for clarity.

spring was found to float on water from 1.5 to more than 7 hours before sinking (unpubl. data). This suggests that seeds carried by the tide could travel many hundreds of meters before coming to rest. Further, a study of seed dispersal on four waterfowl species by Vivian-Smith and Stiles (1994) found *Limonium carolinianum* on the feet and feathers of these birds. Long-distance seed dispersal by animals or by tidal action may be important in founding new populations, either on a new site in the same marsh, or in an entirely different marsh. However, successful colonization due to long-distance dispersal is probably a relatively rare event. The vast majority of the seeds carried by the tide for example, will likely be deposited in water too deep for successful establishment. Only occasionally will the seeds settle in a site suitable for colonization. Long-distance dispersal, although potentially important in founding new populations, will be of little consequence in maintaining local populations in the short term. This was clearly illustrated in the flower harvest experiment by the total lack of seedlings in the picked plots. It is worth noting that these plots were in fact relatively small (5×5 m), and in all cases surround-

ed by plants that successfully set seed. If immigration from long-distance dispersal (i.e., dispersal further than 1 m) is important for local population dynamics, one would expect at least some seedlings to appear in the picked plots. The limited dispersal ability of *L. carolinianum* has also been confirmed by studies of gene flow. Using molecular markers, Hamilton (1997) examined gene flow within and between two *L. carolinianum* populations on Narragansett Bay, Rhode Island. These two populations, located approximately 5 km apart, were genetically distinct. Further, Hamilton observed within-population genetic subdivision at a spatial scale of less than 100 m.

Freshly ripened seeds collected in the fall displayed no innate dormancy; complete germination was achieved when these seeds were placed in a suitable environment in the laboratory. Yet, no germination was observed in the field at this time, suggesting that dormancy was enforced by environmental conditions. Low temperatures are perhaps the most obvious limitation to germination in the fall, but the fact that many seeds remain attached to the inflorescence until spring is probably also important. Seeds attached to the inflorescence will not be able to imbibe sufficient water and will therefore not germinate even with suitable temperatures. Germination in the spring was rapid and synchronous and again, there was no indication that the seeds had any innate dormancy; all seeds that failed to germinate in the laboratory were found to be nonviable. However, viable seeds placed on the marsh after the spring flush of germination failed to germinate in the field, but did germinate (though viability was lower) when brought back into the laboratory. This suggests that any seeds that do not germinate in the spring are prevented from germinating during the summer due to unfavorable environmental conditions, perhaps high salinity levels. Soil salinities increase as the summer progresses in most salt marsh systems (Ungar 1987) resulting in germination inhibition in most halophyte species (Ungar 1994). Snowmelt and periods of precipitation in the spring lower soil salinities, allowing germination to occur for a few weeks in the spring. This pattern of germination is common in halophyte species (Ungar 1994). Given that seeds do not germinate under field conditions in the summer or fall, seeds that do not germinate in their first spring, but are still viable, will not have another opportunity to germinate until their second spring. Our data indicate however that seeds do not survive to their sec-

ond spring under field conditions. Effectively this means that if a seed does not germinate in the first spring after production it will never germinate. As a result, this species lacks a persistent year-to-year seed bank. This conclusion is supported by the fact that no germination was observed in experimental plots that were completely harvested.

Implications for conservation. The lack of a persistent seed bank and the very limited dispersal of *Limonium carolinianum* means that harvesting has an immediate and dramatic effect upon recruitment into the local population. However, whether this in turn would result in significant population declines or lead to the extinction of local populations is as yet unknown. Variation in adult survivorship and growth is often more important than variation in seedling recruitment in determining population growth rate in long-lived species (Caswell 1986). The removal of blooms will divert resources from seed maturation and has the potential to increase adult survivorship and growth. Therefore, it is conceivable that in spite of its marked effect on seedling recruitment, harvesting may in fact have no negative effect on population growth or viability. In addition to information on seedling recruitment, resolution of this question requires long-term data on the effect of harvesting on adult demography and the summarization of these data in the form of a population growth model. We are currently conducting such a study. In the meantime, given that there are anecdotal reports of population declines, it is worthwhile to explore how the results of the present study could be used to help reduce any possible negative effects of harvesting on population viability.

Presently there are no legal means, or voluntary guidelines in existence for managing the harvest of this plant. However, there is growing interest in, and concern over, the sustainable harvest of wild species (Prescott-Allen and Prescott-Allen 1996). Based upon our data we can make two simple recommendations that will help reduce any impact of flower harvesting on *Limonium carolinianum* populations. First, harvesters should never harvest the last inflorescence in a clump of plants. With such a guideline, a population would still have at least one flower stalk per square meter after harvesting. This would ensure that there is some seed available to recolonize a site if the adult(s) in the immediate area should die. Second, periodic closures (voluntary or enforced) of

marshes to flower harvesting would provide pulses of recruitment into a population. If these pulses occur frequently enough relative to the life span of the adults, this would reduce the possibility that local populations would go extinct. Sites where the local population has been extirpated would eventually be recolonized by long-distance dispersal, but our study suggests that natural recolonization would be extremely slow.

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